

# THE SPIRAL BRYOZOAN *TEREBELLARIA* FROM THE JURASSIC OF SOUTHERN ENGLAND AND NORMANDY

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**ABSTRACT.** Morphological study of the monospecific genus *Terebellaria* has determined its unusual pattern of colony growth. Erect, almost cylindrical branches possessed an apical growth tip from which endozonal zooids were budded to extend the branch distally. A helico-spiral growth margin or, less commonly, a succession of annular growth margins, arose from the growth tip and progressed towards the colony base by budding exozonal zooids which were directed proximally so that their distal ends were nearer to the colony base than were their proximal ends. Multilamellar overgrowth of earlier-formed parts of the zoarium was thus achieved. Ontogenetic zones of feeding zooids, with open zooecial apertures and peristomes directed obliquely towards the colony base, occupied bands on the branch apex side of each whorl of the helico-spiral growth margin or each annular growth margin. The creation of a colonial water current system is suggested by this distribution of feeding zooids. Branch proliferation occurred by dichotomy at growth tips and also by 'adventitious' branch formation at exozonal growth margins proximal to the growth tip. By successively re-encrusting its erect branches, growth was relatively efficient, the zoarium was continually strengthened, and the establishment of an exogenous epifauna was hindered.

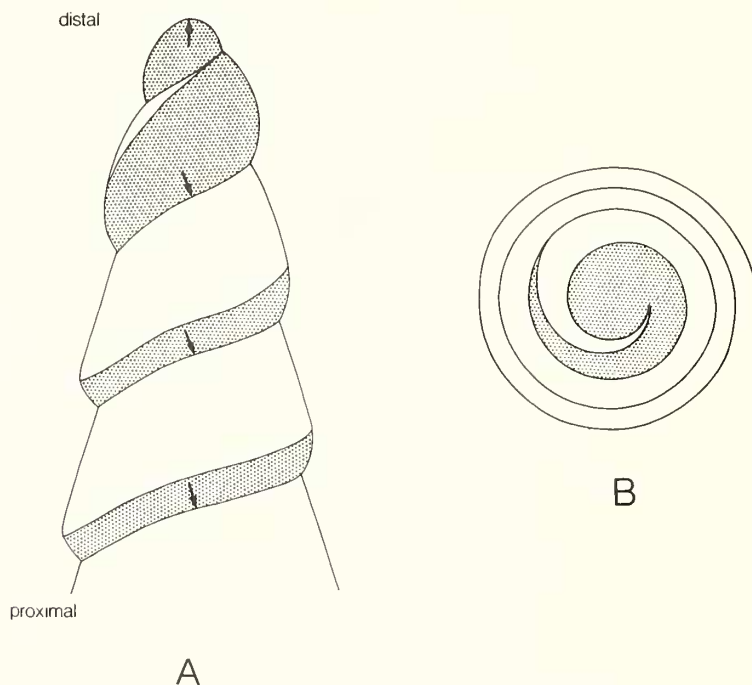
PERHAPS the most distinctive Jurassic bryozoan described is *Terebellaria ramosissima*, the only known species of the genus *Terebellaria*. Its screw-like colonies are particularly abundant in argillaceous basal beds of the English Forest Marble where they are a characteristic component of the well-known 'bradfordian' fauna (Palmer 1974). Because of its rather aberrant appearance, *T. ramosissima* has received attention in a number of works on bryozoans (Boardman and Cheetham 1973; McKinney 1975; Tavener-Smith and Williams 1972), but its three-dimensional morphology has never been fully described nor figured. *Terebellaria* is of further interest since it probably formed the basis on which Gregory (1896a) erected the cyclostome suborder Dactylethrata, which has since been rejected by Walter (1969), Hillmer (1971), and Brood (1972).

## METHODS OF STUDY

External morphology was examined with the aid of a binocular microscope equipped with an eyepiece micrometer for quantitative determinations. Numerous thin sections and cellulose acetate peels were prepared by standard techniques (Boardman and Utgaard 1964; Nye, Dean, and Hinds 1972). Most of the sectioned specimens were initially embedded in an epoxy resin for ease of handling and to ensure that the outer surface of the specimen was preserved during peel preparation. Serial acetate peels at accurately predetermined intervals were obtained with the aid of a Croft grinder. Resin-mounted specimens for examination with the scanning electron microscope were cut and polished, etched with 0.1% formic acid for two minutes, and coated in a ten nanometre layer of gold.

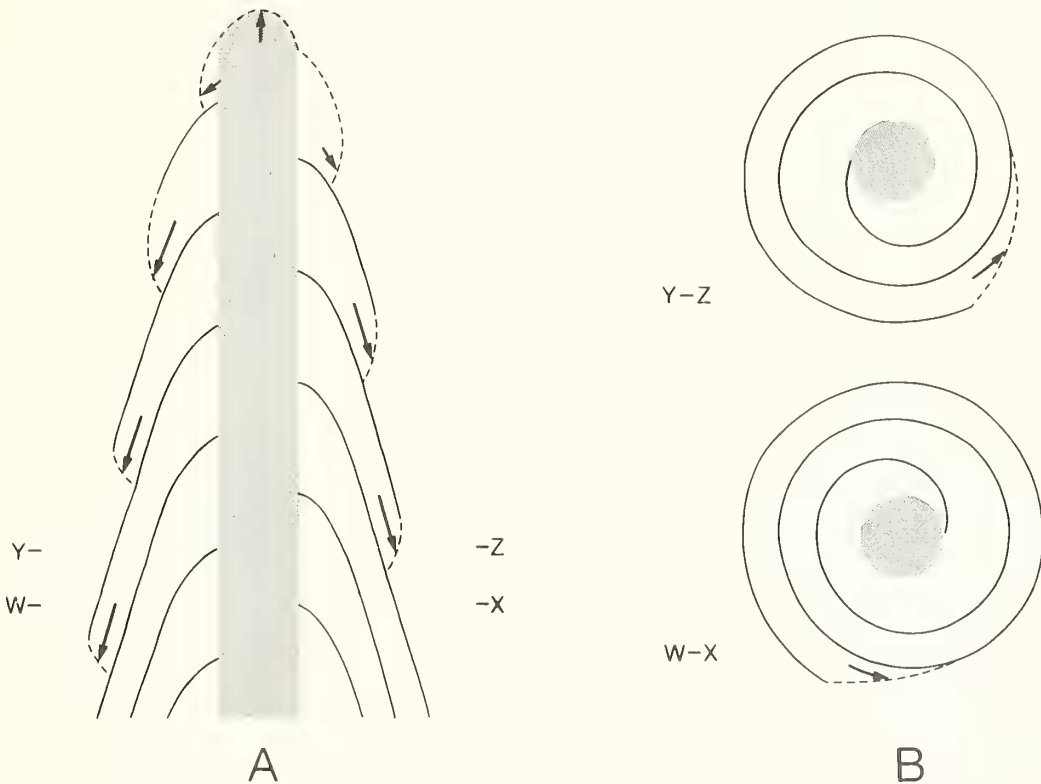
## MORPHOLOGY

*External.* The erect zoarium of *T. ramosissima* (Pl. 34, figs. 1, 7) is usually screw-like in appearance (although some zoaria with a slightly different morphology will be considered later). Diagrams of an unbranched stylized zoarium (text-fig. 1), in which the extreme proximal parts are not shown, are used to illustrate the following morphological description. The proximally broadening screw-like form of the zoarium is defined by the growth margin (see Illies 1968, fig. 11; Taylor 1976, text-fig. 1) of open, partly formed zooecia which forms a series of whorls intervening with a ledge of zooecia complete with frontal walls. Zooecia exposed at the growth margin are directed towards the zoarial base and therefore, contrary to the situation found in most bryozoan colonies, their distal parts are nearer to the zoarial base than are their proximal parts. Zooecia situated between whorls of the growth margin form a shelf which slopes away from the zoarial axis towards the zoarial base. A thin lamina extends from the growth margin towards the zoarial base and covers some of the zooecia forming the shelf. The apex of the zoarium is formed by a growth tip laterally continuous with the screw-shaped or helico-spiral growth margin and similarly composed of open partly formed zooecia. However, open zooecia exposed at the



TEXT-FIG. 1. Simplified external aspects of a helico-spiral branch of *Terebellaria* from which the basal parts have been omitted. Stipple, growth margin and distal growth tip; arrows, directions of colony growth inferred from zooecial orientation. A, lateral aspect. B, colony viewed from above looking down on the growth tip; proximal whorls of the growth margin nearer the branch base are obscured by projecting ledges of zooecia.

growth tip are directed away from the zoarial base so that their distal extremities are also distal with respect to the zoarium as a whole. Both dextral (right-handed) and sinistral (left-handed) branches may occur. The distinction between them is particularly obvious on viewing zoaria from above when the growth margin may be seen to diverge from the growth tip in either a clockwise (dextral) or anti-clockwise (sinistral) manner.



TEXT-FIG. 2. Zoarial sections taken from the helico-spiral branch shown in text-fig. 1. Arrows indicate inferred growth directions at the growth margin and growth tip which are represented by broken lines. Solid lines mark zoecial frontal walls. A, longitudinal zoarial section; the axial region devoid of zoecial frontal walls is the endozone (grey). B, transverse zoarial sections taken at the two levels indicated on the longitudinal section; the origin of the spiral formed by zoecial frontal walls occurs on the periphery of the axial endozone (grey).

*Internal.* Internal structure has been revealed by preparing longitudinal and transverse zoarial sections.

Longitudinal sections show an axial endozone surrounded by a multilamellar exozone (text-fig. 2A). The endozone contains no zoecial frontal walls, lacks a budding lamina, and is exposed externally only at the apical growth tip. Zoecia arising in the endozone do so at divisions of interzoecial walls and are typically obliquely directed distally so that their distal extremities, formed by frontal walls, occur within the exozone. The exozone is laterally continuous with the endozone and, in longitudinal

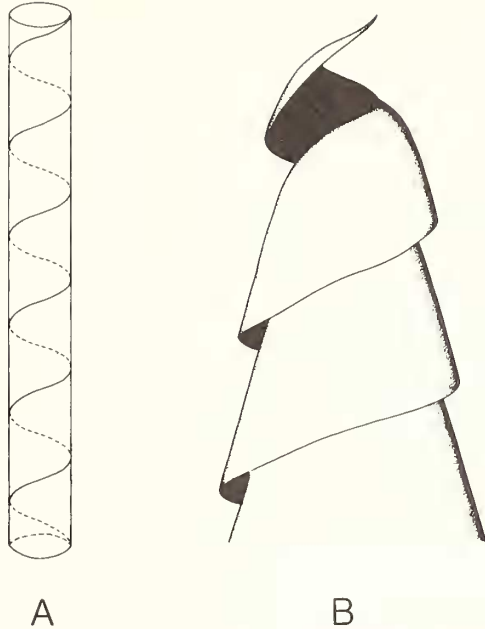
section, its layers appear to arise alternately from either side of the endozone (text-fig. 2A). Hence, endozonally budded zooecia form a series of stacked layers, well-defined distally but indistinct towards the core of the endozone. Endozonal zooecia within each layer are arranged so that the nearer the zoarial base they arise, the closer to the zoarial apex they terminate (text-fig. 7). Those arising nearer the base diverge at a small angle to the zoarial axis, but more distally arising zooecia may be reflexed by up to about  $90^\circ$  until they become perpendicular to the zoarial axis (Pl. 35, fig. 2). The most proximally arising, and thus most distally terminating, zooecia of each endozonal layer are for convenience here termed the 'omega' zooecia, although this does not imply that they are necessarily heterozooecia. More distally arising exozonal layers, bounded by a budding lamina and zooecial frontal walls, partly cover those which arise nearer the zoarial base. Successive exozonal layers terminate at consecutive whorls of the helico-spiral growth margin, as may be seen in longitudinal sections. Exozonal zooecia differ from those of the endozone because they arise at the junction between budding lamina and an interzooecial wall. Although longitudinal zoarial sections cut both endo- and exozonal zooecia longitudinally, those zooecia arising in the core of the endozone, including the omega zooecia, are somewhat obliquely sectioned because they are slightly twisted in the direction of spiral coiling of the zoarium.

Transverse zoarial sections (text-fig. 2B) show that the endozone, which appears to be a series of discrete layers when seen in longitudinal section, forms a continuous spiral in which later whorls overlap earlier ones. The budding lamina on which exozonal zooecia arise covers frontal walls of earlier zooecia in previous whorls (Pl. 35, fig. 5). The lamina describes an almost equable spiral (Thompson 1961, pp. 175–176) and has an eccentric origin on the surface of the axial endozone. Viewed from above, lamina spirals visible in transverse section (Pl. 35, fig. 1) may be either sinistral or dextral. However, the direction of spiral coiling will be opposite to that of the helico-spiral shape seen externally (cf. text-figs. 1B and 2B). Successive serial transverse zoarial sections show that the point of origin of the budding lamina rotates around the perimeter of the endozone. If the spiral seen in transverse section is sinistral, then its point of origin rotates in an anticlockwise direction between successively more distal sections towards the zoarial apex. If the spiral is dextral, then its point of origin rotates in a clockwise direction distally towards the zoarial apex. Most of the exozonal zooecia and centrally situated endozonal zooecia are cut transversely by zoarial transverse sections. However, the more reflexed endozonal zooecia, with long axes perpendicular to the zoarial axis, and some contiguous zooecia, are cut longitudinally by transverse zoarial sections (text-fig. 6A). The same zooecia are twisted slightly in the direction of the spiral described by the budding lamina. Thus, transverse zoarial sections reveal a distinctly asymmetrical arrangement of zooecia (Pl. 35, fig. 1). In a given transverse section, narrow proximal portions of astogenetically younger endozonal zooecia occur mainly on the axial side of the large omega zooecia in the vicinity of the exozonal origin point (text-fig. 6A). The narrow proximal portions of exozonal zooecia are observed where interzooecial walls bifurcate at their junction with the budding lamina.

*Three-dimensional synthesis.* The endozone forms an axial cylinder within which neither zooecial frontal walls nor a budding lamina occur. The axis of the endozonal cylinder is probably slightly helically twisted so that it attains an appearance



TEXT-FIG. 3. Three-dimensional aspects of the helico-spiral branch shown in text-figs. 1 and 2. A, the helical exozonal trace which represents the line along which axial walls of omega endozonal zooecia meet the periphery of the endozone and gave rise to the exozonal budding lamina; shown solid when on the near side and dashed when on the reverse side of the cylindrical endozone. B, surface formed of zooecial frontal walls over which the exozonal budding lamina subsequently extends; its inner edge is the helical exozonal trace, its outer edge occurs at the growth margin which extends towards the colony base during growth.



approaching that of the complete *Zonopora* zoarium (Nye 1976, pl. 147). In *T. ramosissima*, the endozone is visible externally only at the hemispherical growth tip where new endozonal zooecia arise and diverge such that their distal parts occur within the exozone. Exozonal zooecia arise at the margin of a basal budding lamina, which extends as a helico-spiral coil towards the zoarial base partly covering previously formed zooecia. The point at which the exozone emerges from the surface of the cylindrical endozone is defined by the appearance of the budding lamina. The axial edge of this lamina describes a helical trace, here termed the exozonal trace, on the surface of the endozone (text-fig. 3A). Both sinistral and dextral exozonal trace helices are known in *T. ramosissima* and the direction of helical coiling determines directly whether the helico-spiral seen externally is sinistral or dextral. The form of the laminate surface composed of zooecial frontal walls (text-fig. 3B) reveals the involved three-dimensional morphology of the exozone.

#### SPIRAL GROWTH

Growth in bryozoan colonies is achieved largely by zooidal addition. Borg (1926) showed that zooidal budding in extant cyclostomatous bryozoans occurs in regions of the colony enclosed beneath a common or hypostegal coelom which he termed the 'common bud'. Here, interior body walls are secreted by epithelial tissue which lines them on both sides (Boardman and Cheetham 1973). New zooids are partitioned off by division of these interzooidal walls. Elsewhere hypostegal coelom is lacking and zooidal budding does not usually occur (cf. peristomal budding described by Harmelin 1974). Zooidal growth away from the common bud is limited to the lengthening of exterior body wall, such as peristomes and zooecial frontal walls, secreted from one

side only. In fossil tubuloporinidean cyclostomes partly formed zooecia with incomplete frontal walls (exterior body wall) and having their interzooecial walls (interior body wall) exposed are characteristic of regions in which zooidal budding was occurring during life. By analogy with extant taxa, these regions were covered by hypostegal coelom. The helico-spiral growth margin and apical growth tip clearly constituted the common bud of *T. ramosissima* colonies and were enclosed beneath a continuous hypostegal coelom within which new zooids became partitioned off by the division of expanding interior body walls. Zooidal budding caused the growth margin and growth tip to advance and leave behind zooids, no longer in coelomic continuity with one another, which are represented by those zooecia occupying the ledge between whorls of the helico-spiral growth margin.

The morphology of *T. ramosissima* contrasts with that of most other erect tubuloporinidean cyclostomes which have an apical growth tip from which zooecia are budded to lie in a distally divergent orientation. This morphology characterizes so-called vinculariiform zoaria such as *Pustulopora* (Brood 1972, p. 95) where zooidal budding does not occur proximal of the growth tip. Transverse zoarial sections are almost identical to those aspects of the zoarium seen by looking down on the growth tip. Successively more distal transverse sections approximate to discrete growth stages for no further zooecia can be added in the plane of section. However, the helico-spiral growth margin of *Terebellaria* is intersected by all transverse zoarial sections and transverse sections do not thus correspond to distinct growth stages for further zooecia may be added in the plane of section. In addition, external aspects of the zoarium seen by looking down on the growth tip do not approximate in appearance to transverse zoarial sections (cf. text-figs. 1B and 2B).

*Zooecial budding.* Two distinct modes of zooecial budding occurred in *Terebellaria* colonies. At the apical growth tips of the colony endozonal zooecia were budded by division of interzooecial walls at triple junctions between established zooecia. Newly budded zooecia occupy space partitioned off from more than one established zooecium, a budding style termed interzooecial by McKinney (1975). Endozonal zooecial budding had a locus on the axial walls of omega zooecia (text-fig. 8).

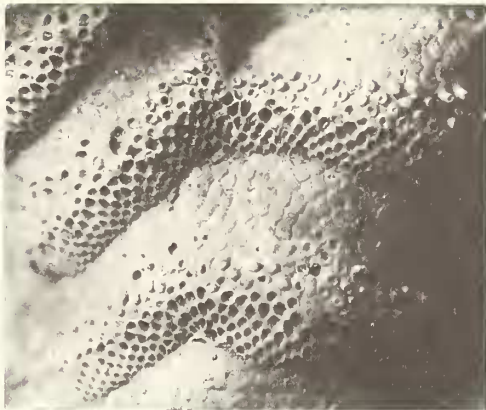
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#### EXPLANATION OF PLATE 34

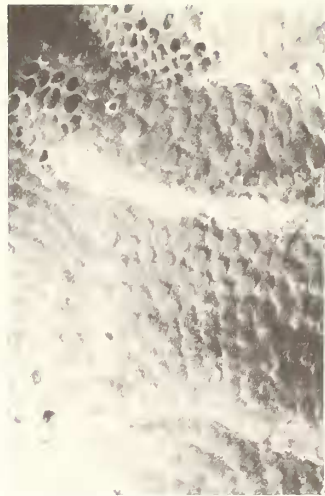
Figs. 1-9. *Terebellaria ramosissima* Lamouroux. Bathonian. 1, BMNH 11510c, distal portion of a dextral branch showing the apical growth tip and helico-spiral growth margin. ?locality,  $\times 7$ . 2, BMNH D4518, parts of three growth margins proximal to a branch dichotomy showing ontogenetic zonation of zooecia, Ranville,  $\times 8$ . 3, BMNH 60215, portion of a zoarium in which all zooecia and the growth margin (centre) are occluded, Ranville,  $\times 10$ . 4, BMNH 11510d, the opposite end of the horizontal growth margin division shown in text-fig. 9. A zoarial lateral wall extends across the dislocation (arrowed), ?locality,  $\times 7$ . 5, BMNH 60215d, zoarial fragment with a branch dichotomy, Ranville,  $\times 2.3$ . 6, BMNH 60360b, adventitious branch (right) arising from a parent branch with occluded growth margins, Ranville,  $\times 7$ . 7, BMNH D1812q, incipient dichotomy at the tip of a dextral branch, Bradford-on-Avon,  $\times 7$ . 8, BMNH D52637, ovicell with ooeciopore (arrowed), St. Aubin-sur-mer,  $\times 15$ . 9, BMNH 60360a, zoarium showing a common preservation in which the zooecial frontal walls have been removed by abrasion, Ranville,  $\times 6$ .



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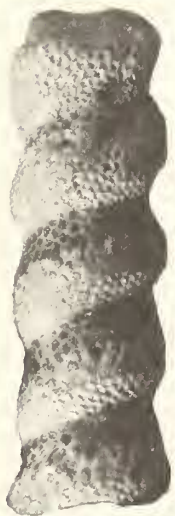
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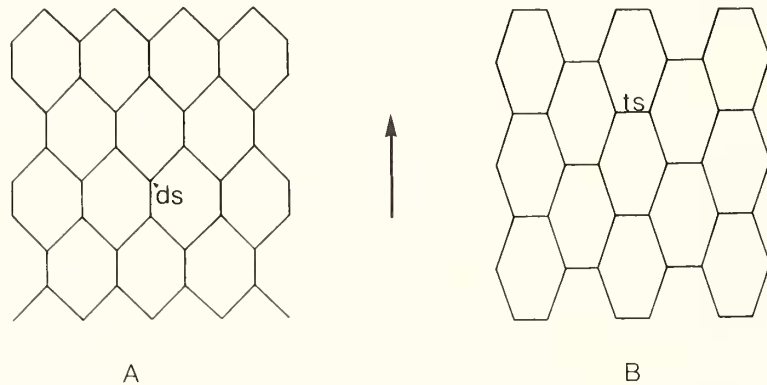


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TAYLOR, *Terebellaria ramosissima*



Exozonal budding at the helico-spiral growth margin occurred within a basal prolongation of the same hypostegal coelom as that which covered the growth tip. However, exozonal zooecia were budded at junctions between interzooecial walls and the budding lamina. The budding lamina was apparently an exterior body wall of the type which invariably exists at the attached bases of cyclostome colonies. The pattern of zooecial budding on this lamina compares with that known in many other cyclostome taxa (Borg 1926; Boardman and Cheetham 1973; Illies 1968). An almost perpendicular rudimentary interzooecial wall, or septum, divides where it meets the budding lamina producing a triangular cavity forming the proximal part of a zooecium. During further growth the cavity enlarges until its sloping interzooecial lateral walls coalesce with identical walls belonging to adjacent zooecia. Such coalescence causes the formation of a vertical interzooecial wall of a new generation. This type of budding pattern produces a characteristic pattern of septal traces which delineate the basal parts of elongate hexagonal zooecia developing on the budding lamina (text-fig. 4A). The long axis of each zooecium bisects the angle formed between pairs of oblique distal and proximal walls. The septal trace pattern is frequently repeated where the interzooecial walls meet the frontal surface of the zoarium. An alternative type of septal trace pattern (text-fig. 4B) predominates in *T. ramosissima*. It results from new zooecia being partitioned off by the formation on the budding lamina of a transverse septum linking two previously formed vertical septa. The transverse septum slopes upwards to meet the zoarial surface distally. Long axes of zooecia bisect



TEXT-FIG. 4. Septal trace patterns formed where interzooecial walls meet a basal budding lamina. The pattern is usually repeated distally where the interzooecial walls contact the zoarial surface formed of zooecial frontal walls. Growth direction is indicated by an arrow. A, normal tubuloporinidean septal trace pattern. New zooecia are partitioned off by division of an established interzooecial wall or septum (ds). In plan, zooecia are hexagonal with their long axes bisecting, both proximally and distally, the angle made between pairs of oblique interzooecial walls. B, alternative septal trace pattern common in *Terebellaria*. The formation of an inclined transverse septum (ts) partitions off a new zooecium. As a result, zooecia are hexagonal with their long axes bisecting, both proximally and distally, interzooecial walls or septa which lie transverse to growth direction.



transverse septa at both ends of elongate hexagonal zooecial bases. Borg (1926, fig. 39, septum 'y') noticed that zooecial budding of this type occurred occasionally in normal tubuloporinidean budding patterns where it produced zooecial proliferation by intercalating an additional zooecium.

Endozonal and exozonal zooecia are not considered to be polymorphically distinct from one another despite their different budding modes. There is continuous variation in quantitative morphological characters between the most axial endozonal zooecia (omega zooecia) and exozonal zooecia. By analogy with extant cyclostomes, exozonal zooecia are certainly autozooecia and occasional preservation of conventional peristomes in endozonal zooecia suggests that they too are autozooecia.

*Growth pattern.* To determine patterns of growth in fossil cyclostomes it is necessary to recognize the regions in which zooids were being budded immediately prior to colony death, and to infer previous positions and attitudes of zooidal budding regions. As growth in all bryozoans occurs in a proximal to distal direction, the direction of local colony growth may be determined by recognizing the proximal and distal parts of zooecia. *T. ramosissima* zooecia are narrow proximally but become broader distally and develop a frontal wall with a distal aperture where they rise obliquely to meet the zoarial surface. Exozonal zooecia are usually orientated with their long axes almost parallel to the zoarial long axis, and with their distal ends closer to the zoarial base, indicating that they grew towards the colony base. Conversely, endozonal zooecia typically have their distal ends nearer to the zoarial apex, indicating growth away from the colony base. The attitudes of preserved budding regions confirm these conclusions for exozonal growth margins face the zoarial base, but the endozonal growth tip is directed away from the zoarial base (text-fig. 1A). Therefore, exozonal growth towards the colony base accompanied endozonal growth, extending the colony distally.

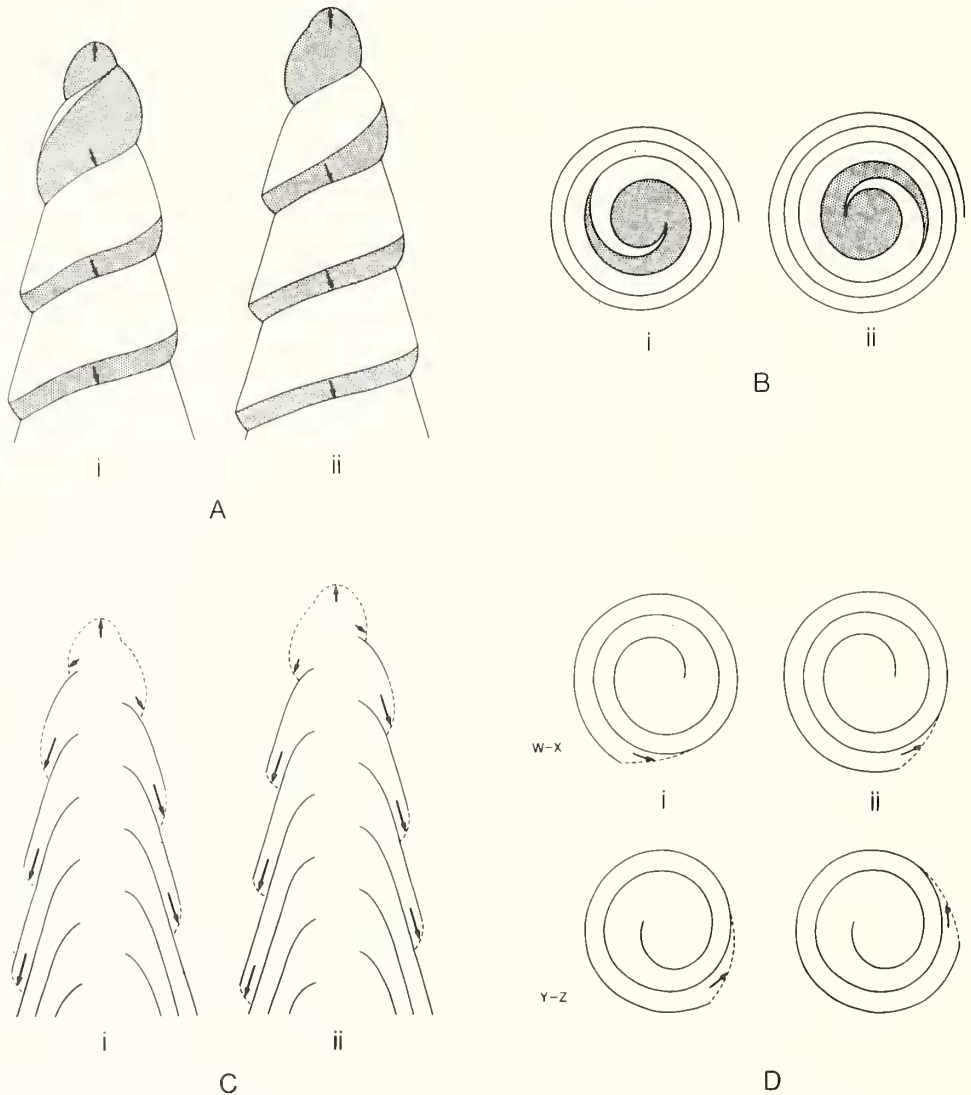
Long axes of endozonal zooecia meet the surface of the almost hemispherical growth tip at right angles. Zooecia are asymmetrically distributed over the growth tip with respect to their size. Smaller, more recently budded, zooecia are concentrated slightly axially of large omega endozonal zooecia of the preceding helical whorl. Hence, the locus of endozonal budding is eccentrically situated relative to the central axis of the zoarium. Distal colony extension apparently caused rotation of the locus of endozonal budding in unison with the point of exozonal origin.

The essentially linear helicospiral growth margin compares with growth margins known from many adnate tubuloporinidean taxa. Long axes of newly budded zooecia are perpendicular to the length of the growth margin and thus make a small angle with the long axis of the *T. ramosissima* zoarium. A helico-spiral growth margin was typically maintained throughout growth, but its whorls progressed towards the colony base whilst the helico-spiral was lengthened as endozonal growth extended the colony distally.

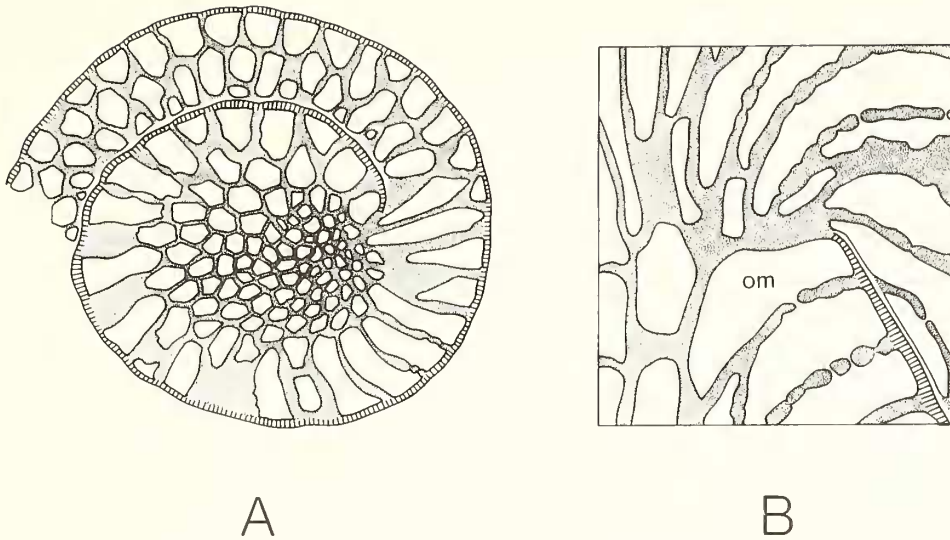
To illustrate the inferred mode of colony growth, an arbitrary increment of growth (text-fig. 5) has been added to the stylized zoarium originally shown in text-figs. 1 and 2. Exterior lateral aspects (text-fig. 5A) show the simultaneous effect of distal colony extension and basalward exozonal growth, which lengthen and broaden the zoarium respectively. The position of divergence from the growth tip of the helico-spiral growth margin, and the locus of endozonal budding, both rotate by 180° in a clockwise

direction when the growth increment is added (text-fig. 5B). Translation produced by distal colony extension combined with this rotatory motion cause the exozonal trace to be helical in form (text-fig. 3A). Comparison of transverse sections cut at equivalent positions on the zoarium before and after addition of the growth increment (text-fig. 5D) show clockwise extension of the overgrowing spiral exozone.

Variations in over-all proportions observed between natural zoaria can be related to variations in the relative growth rates of endozone and exozone, or to the rate of



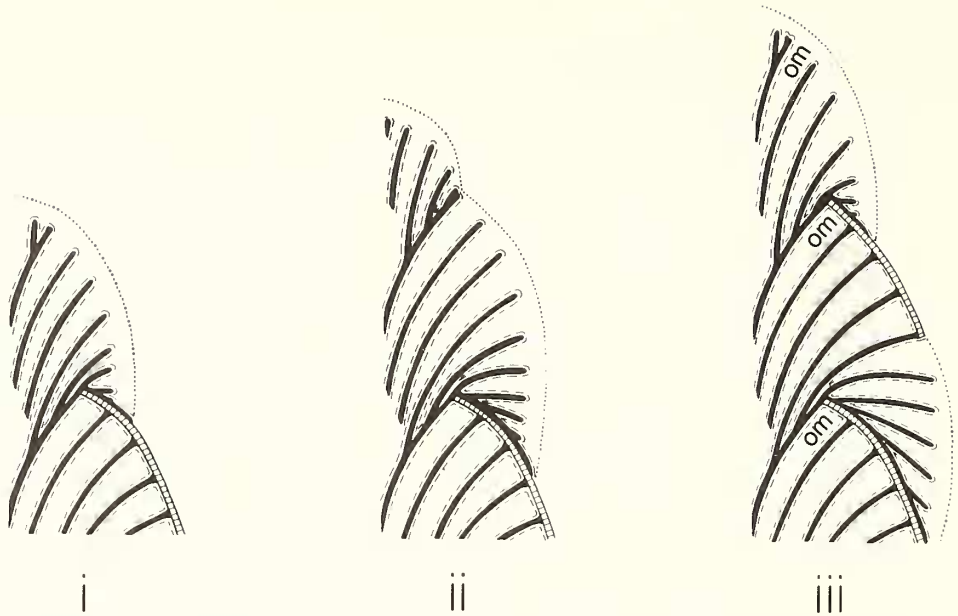
TEXT-FIG. 5. Addition of an arbitrary increment of growth to the helico-spiral branch illustrated in text-figs. 1-3. In all cases diagrams labelled 'i' are before growth, 'ii' after growth. A, external lateral aspects. B, external aspects viewed from above the distal growth tip. C, longitudinal zoarial sections. D, transverse zoarial sections.



TEXT-FIG. 6. Camera lucida drawings to illustrate zoecial configuration in sections of helico-spiral branches of *Terebellaria ramosissima*. Stipple, interzoecial walls; white, basal budding lamina; hatched, zoecial frontal walls. A, part of transverse zoarial section showing an axial endozone, lacking zoecial frontal walls, in which zoecia are sectioned approximately transversely. The endozonal budding locus is the region occupied by the smallest zoecia. Strongly reflexed zoecia near to the boundary between endozone and exozone are almost longitudinally sectioned; BMNH D2111g, 'Bathonian, Ranville'.  $\times 19$ . B, part of a longitudinal section at the transition between endozone and exozone. The axial interzoecial wall of an omega endozonal zoecium (om), slightly obliquely sectioned, gives rise to its own frontal wall (stippled) and the exozonal budding lamina which covers it. Endozonal budding has a locus above the axial wall of the omega zoecium. Interzoecial walls have pores and constrictions; BMNH D2111j, 'Bathonian, Ranville'.  $\times 39$ .

rotation of the exozonal origin point. If the endozone grew more rapidly than the exozone a slender zoarium resulted, whilst the converse situation would have produced a zoarium broadening rapidly towards its base. A relatively rapid rotation of the exozonal origin point would have produced a tight exozonal helical trace and a zoarium in which the distance between successive whorls of the helico-spiral growth margin is small.

*Transition zone interpretation.* The zone of transition between endozone and exozone (Pl. 35, fig. 4) deserves further attention, for here the mode of zoecial budding altered and a partial splitting or 'unzipping' of the colonial common bud may be inferred. The nature of the transition is explained by reference to text-fig. 7, which shows a growth series of longitudinal half sections on which are marked probable positions of epithelia during life. At growth stage 'i' extension of endozonal zoecia was occurring by distal growth of interzoecial walls beneath the hypostegal coelom of the growth tip. Zoecia which later contributed to the endozone of the succeeding helical whorl were budded off predominantly from the axial wall of the omega zoecium in the plane of section (text-fig. 6B). When interzoecial walls of the omega zoecium contacted the



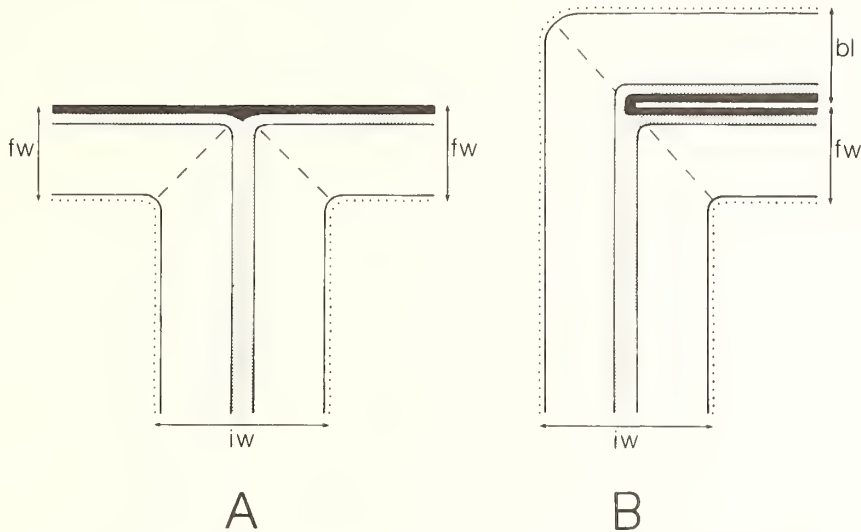
TEXT-FIG. 7. Interpretation of growth at the transition between endozone and exozone in *Terebellaria*. Longitudinal half sections of three growth stages, 'i'-'iii'. For detailed explanation of the sequence of events see text. Interzoecial walls and budding lamina, black; zoecial frontal walls, hatched; inner epithelium lining interzoecial walls, dashed line; outer epithelium, dotted line; omega zooecia, om. The hypostegal coelom of the common bud (growth tip and growth margin) is enclosed between the inner and outer epithelia. Zooecial apertures have been omitted for simplicity.

outer epithelium (growth stage 'ii') the zooecium lost hypostegal coelomic connection and growth of its frontal wall began. This contact with the outer epithelium delineates the outer surface of the cylindrical endozone. Further endozonal zooecia of the same helical whorl, but progressively nearer the colony base, also contacted the terminal membrane and began to form frontal walls. In this way, within the plane of section, the hypostegal coelom of the growth tip had become separated from that of the basally extending growth margin by an intervening area of zooecia which possess calcified exterior body walls. Laterally contiguous exozonal zooecia then also began to form calcified exterior body walls (growth stage 'iii'). Endozonal zooecia of the succeeding helical whorl had continued to extend upward by lengthening their interzoecial walls beneath the hypostegal coelom of the growth tip. At the same time, exozonal zooecia were formed on a budding lamina which began to overgrow the frontal wall of the omega zooecium from the preceding helical whorl. The budding lamina thus appears to develop immediately above the position at which the frontal wall of the omega zooecium from the preceding helical whorl met the endozone. The lamina is of course laterally continuous off the plane of section, with the lamina flooring exozonal zooecia budded in previous whorls of the helix. As the lamina extended towards the colony base zooecia of the exozone were budded on it.

The helical exozonal trace (text-fig. 3A) is the line along which diverging axial



interzoecial walls of omega zooecia meet the surface of the cylindrical endozone. At this contact each interzoecial wall bifurcates to form the frontal wall of the omega zooecium and the exozonal budding lamina which subsequently overgrows that frontal wall. The exozonal budding lamina is apparently a type of exterior body wall homologous with the basal laminae, upon which cyclostome colonies are commonly founded. Hence, when the axial interzoecial wall, an interior body wall, of the omega zooecium contacts the surface of the endozone it divides to form two exterior body walls of different type, a zoecial frontal wall and a budding lamina. An analogy may



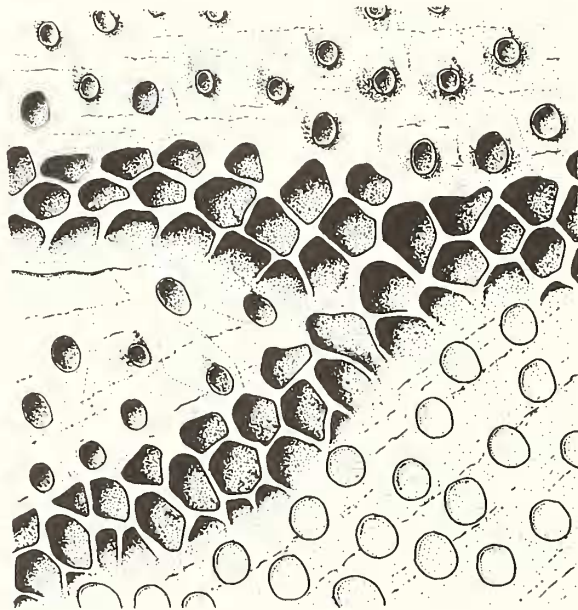
TEXT-FIG. 8. Dichotomies of interzooidal walls (interior body wall) to form two exterior body walls. A, normal type of dichotomy (after Brood 1972, fig. 7D; Hinds 1975, text-fig. 1). The interzooidal wall (iw) is composed of a primary skeletal layer (stippled) flanked by secondary skeletal layers (white) bordered by secretory epithelia (dotted line). It divides to form two zoecial frontal walls (fw) composed of a surficial cuticle (black) underlain by a primary skeletal layer, which overlies a secondary skeletal layer and secretory epithelia. Arbitrary boundary between the interzooidal wall and the frontal walls is a dashed line. B, dichotomy inferred to have occurred in the omega zooecia of *Terebellaria* when their interzooidal walls met the periphery of the endozone. The interzooidal wall (iw) divides to form a zoecial frontal wall (fw) and a basal budding lamina (bl) which subsequently covers the frontal wall.

be made between this division and that commonly observed in which an interzoecial wall divides to give two zoecial frontal walls (text-fig. 8A). If one of the frontal walls is rotated by  $180^\circ$  until it lies directly upon the other (text-fig. 8B) then the situation occurring at axial omega zooecial wall division in *T. ramosissima* is achieved. The rotated frontal wall apparently must now become an exterior body wall of the basal lamina type for its cuticle is juxtaposed with a substratum, the frontal wall of the adjacent zooecium. The omega zooecium began to be overgrown by the budding lamina soon after its frontal wall had formed, but frontal wall formation in zooecia nearer the colony base progressed more rapidly than extension of the budding lamina and a separation of about 2 mm was achieved.

Occasionally the exozonal growth margin divided into two in a plane parallel to the budding lamina by the formation of a new budding lamina midway between the original lamina and the frontal surface of the zooecial layer. This type of division (text-fig. 9) probably also required bifurcation of an interzooecial wall to form a zooecial frontal wall and a new, overgrowing, budding lamina. The dichotomy contrasts with that of omega zooecial axial walls because the growth margin beneath grew more rapidly than that above the division. Such horizontal growth margin division began at a particular point and spread laterally along the growth margin in one direction only. Meanwhile, distal growth from the initial point of appearance of the split caused the formation of a zoarial lateral wall (Pl. 34, fig. 4) comparable to those produced by migrating pivot points in other cyclostomes (Taylor 1976, p. 302). Growth margin horizontal division apparently also occurs in the extant bereniciform species *Plagioecia platydiscus* described by Harmelin (1976).

#### ANNULAR GROWTH

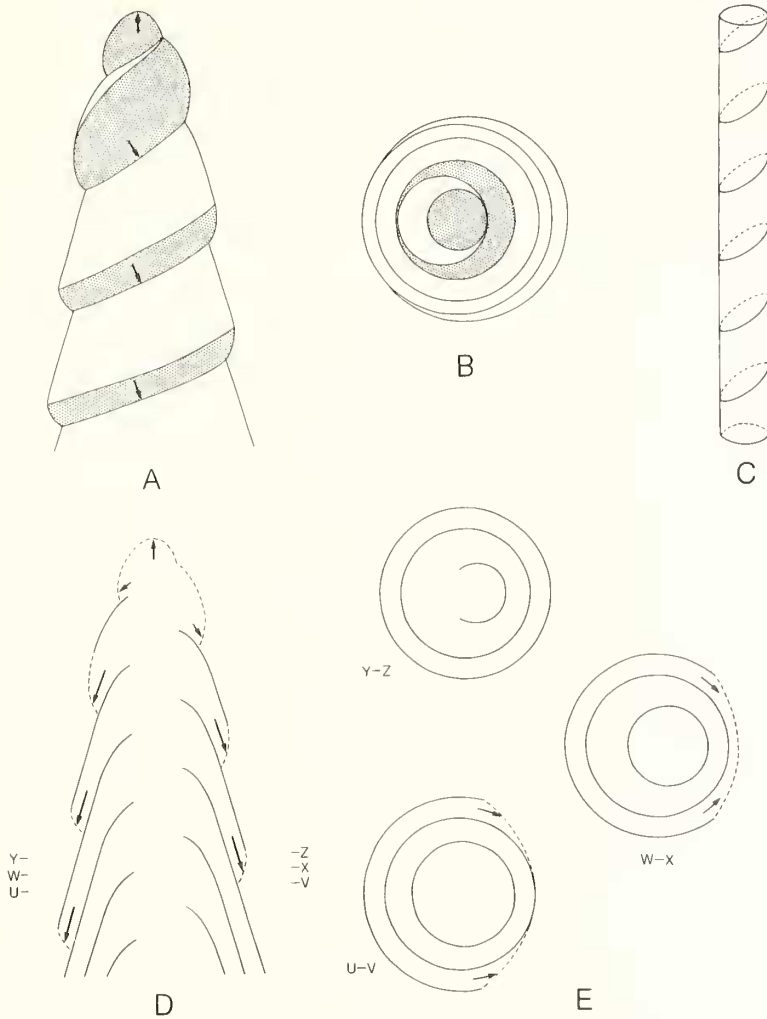
Although the exozonal growth margin in *T. ramosissima* is normally a helico-spiral, a second situation may occur in which the exozone is composed of a series of discrete ring-shaped or annular growth margins. Branch dichotomies frequently result in at least one of the daughter branches having exozonal growth margins of this type. Annular growth margins are about the same distance apart as the successive whorls of



TEXT-FIG. 9. Camera lucida drawing showing part of the exterior of a *Terebellaria ramosissima* zoarium in which horizontal division of the growth margin was occurring. A split in the growth margin was apparently extending from left to right; BMNH 11510d, 'Great Oolite ?locality'.

× 34.

a helico-spiral growth margin, and they are usually inclined with respect to the zoarial axis. Transverse zoarial sections, instead of revealing a spiral exozone, show discrete exozonal layers, each floored by a budding lamina, arranged in an off-centred concentric pattern (text-fig. 10E). The number of concentric zoecial layers present in a transverse section indicates the number of growth margins which have overgrown that part of the colony. Longitudinal zoarial sections (text-fig. 10D) may be indistinguishable from similar sections taken from branches with helico-spiral growth margins.



TEXT-FIG. 10. *Terebellaria* branch with an annular exozone. Legend as in text-figs. 1-3. A, external lateral aspect. Compare with text-fig. 1A. B, external aspect looking down upon the distal growth tip. Compare with text-fig. 1B. C, inclined annular exozonal traces occurring on the periphery of the cylindrical endozone. Compare with text-fig. 3A. D, longitudinal zoarial section. Compare with text-fig. 2A. E, transverse zoarial sections taken at the levels marked on the longitudinal section. Compare with text-fig. 2B.

Colonies have the same cylindrical endozone as those possessing a helico-spiral growth margin, and have zooecia typically directed distally in the endozone and basally in the exozone. In three dimensions the exozonal layers take the form of a series of stacked cones truncated where they meet the endozone. Traces on the cylindrical endozone marking the point of origin of the exozone are thus a succession of inclined rings (text-fig. 10C). Some transverse zoarial sections reveal two points of origin for the innermost exozonal layer, whilst others have no points of exozonal origin. Sections of the former type are located at positions where the innermost off-centred budding lamina intersects the cylindrical endozone and is crescent-shaped. Those of the latter type occur at positions which have no such intersections and the innermost budding lamina is annular.

Stylized diagrams (text-fig. 10A, B) illustrate the external appearance of a branch with annular growth margins. Transverse zoarial sections have been cut serially in the direction of distal colony extension (text-fig. 10E). In section U-V the innermost budding lamina forms a complete ring for it has no intersection with the endozone. The diameters of all budding laminae decrease distally towards the branch apex, in accordance with their conical three-dimensional form, until in section W-X the innermost budding lamina almost intersects the left side of the endozone. Distal to W-X this innermost lamina is crescent-shaped and has two points of exozonal origin in the plane of section. Its diameter continues to decrease towards the colony apex, for example at section Y-Z. The budding lamina last occurs at the extreme right of the endozone before disappearing from the plane of section. The diameters of other exozonal rings also decrease distally, and the lamina which is now innermost occupies a position equivalent to that of the innermost lamina in section U-V.

Longitudinal zoarial sections (text-fig. 10D) reveal an identical mode of derivation of the exozone from the endozone in both spiral and annular growth. In branches displaying an annular exozone the endozone can again be partly divided into layers. Each layer is produced by endozonal zooecial budding centred on axial walls of omega zooecia belonging to the preceding layer. However, exozone was produced continuously in branches with a helico-spiral growth margin, but discontinuously in those with annular growth margins where periods of new exozonal layer formation at the growth tip would have alternated with intervals of endozonal extension without formation of new exozonal layers. By inference, hypostegal coeloms enclosing individual growth margins became successively divided from the hypostegal coelom covering the growth tip.

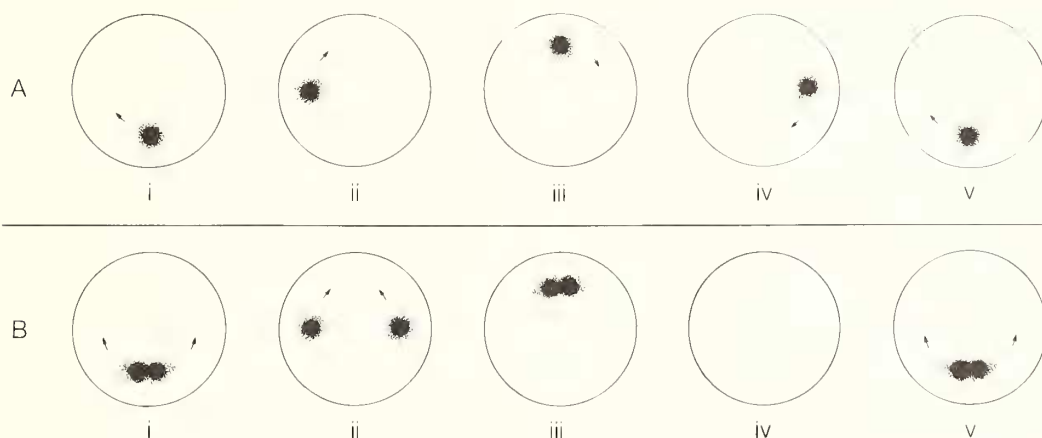
The distinction between branches with a helico-spiral growth margin and those with annular growth margins may be explained in terms of movement of the endozonal budding locus. The type of movement apparently dictated the form of the exozonal trace which in turn determined zoarial external appearance. Rotation of the endozonal budding locus in one direction only, combined with the translatory motion of distal growth (text-fig. 11A), would produce a helical exozonal trace and a helico-spiral growth margin. Distal growth accompanied by division of the endozonal budding locus, followed by rotation of the two consequent loci in opposite directions and their eventual meeting at the other side of the endozone (text-fig. 11B) would produce a branch with annular exozonal traces and annular growth margins.



## BRANCH PROLIFERATION

There are two distinct modes of branch proliferation in *T. ramosissima*. Primary branching occurred by dichotomy at apical growth tips, and secondary or adventitious branching by development of daughter branches at exozonal growth margins.

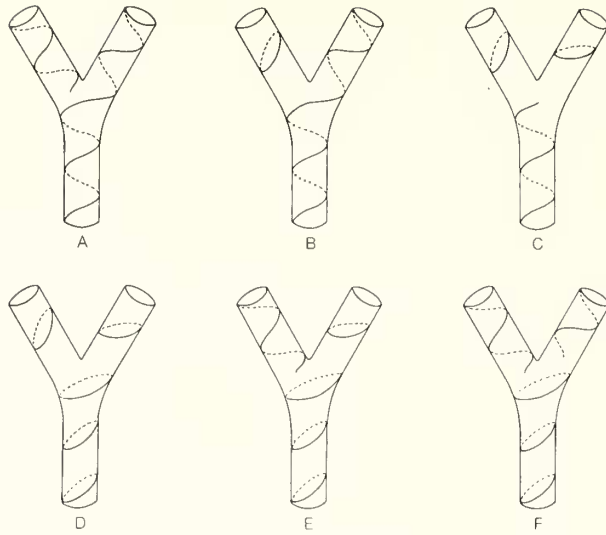
*Primary branching.* Equilateral division at the branch apex formed two daughter branches which diverged from one another at an angle between  $30^\circ$  and  $70^\circ$  (Pl. 34, fig. 5). Zoarial sections show that branch dichotomy involved a splitting of the cylindrical endozone. Immediately prior to division, the endozone became elliptical in cross-section by increasing its diameter within the plane in which the division was to



TEXT-FIG. 11. Diagrammatic transverse zoarial sections showing rotation of the budding locus (stippled) within the circular endozone during distal branch extension in *Terebellaria*. Five growth stages, 'i'-v'. A, clockwise rotation giving rise to a branch which is a dextral helico-spiral externally. B, division of the locus and rotation of the two consequent loci in opposite directions prior to their coalescence at the opposite side of the endozone. A new locus forms after an interval of time in which there is no endozonal budding locus. A branch with inclined annular growth margins is produced by this sequence of events.

occur. Subsequent constriction of the ellipse midway along its major axis culminated in eventual division of the endozone into two. This pattern of endozonal division is also characteristic of other cyclostomes possessing cylindrical branches with apical growth tips. In *T. ramosissima*, however, the presence of a layered exozone complicated the growth pattern produced by dichotomy.

The effect on the exozone of endozonal dichotomy is most suitably examined by considering changes in the form of the exozonal trace. The parent branch may have either a helical or an annular exozonal trace reflecting spiral and annular modes of growth respectively. Both daughter branches may have helical or annular exozonal traces, or one may have a helical and the other an annular exozonal trace. Therefore,

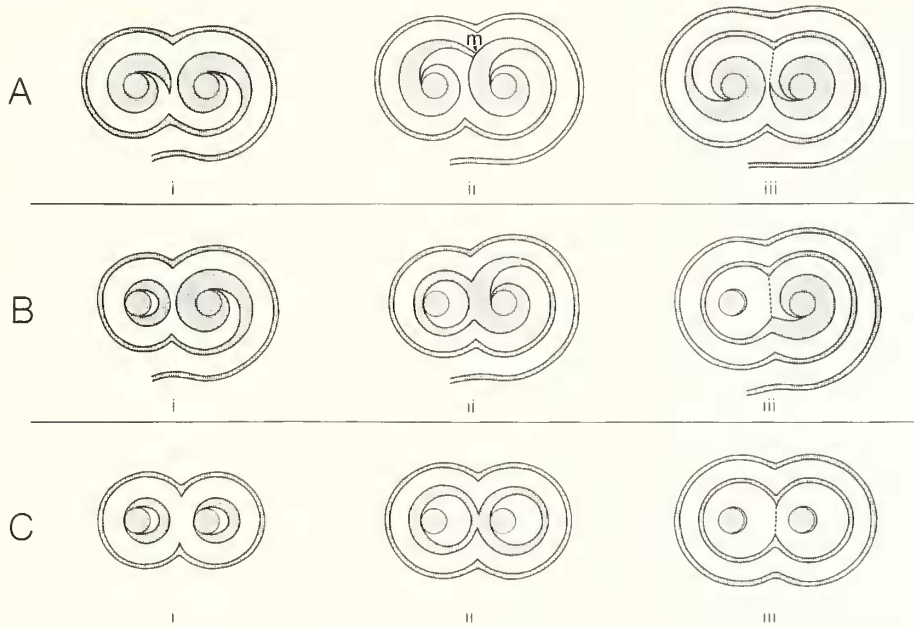


TEXT-FIG. 12. The six possible modifications of the exozonal trace consequent upon primary branching. A, B, and E have been positively identified in fossil zoaria. A, parent branch and both daughter branches have helical traces. B, parent branch and one daughter branch have helical traces, the second daughter branch has annular exozonal traces. C, parent branch has a helical trace, both daughter branches have inclined annular traces. D, parent branch and both daughter branches have annular traces. E, parent branch and one daughter branch have annular traces, the second daughter branch has a helical trace. F, parent branch has an annular trace, both daughter branches have helical traces.

there exist six alternatives for exozonal trace pattern changes during dichotomy (text-fig. 12). Types A, B, and E of text-fig. 12 have been positively identified in fossil zoaria. In types A, E, and F new helical exozonal traces had to be initiated on one or both daughter branches after endozonal division. This was achieved by the formation of a new series of omega zooecia whose axial walls on reaching the outer epithelium gave rise to frontal walls and a budding lamina. The exozonal trace on the parent branch of types A and E apparently continues up one of the daughter branches. If one or both of the daughter branches display spiral growth it is always in the same spiral direction (sinistral or dextral) as that of their parent branch. In this respect, *Terebellaria* differs from two other well-known bryozoan genera which exhibit spiral growth forms. In both *Archimedes* (Condra and Elias 1944; Cowen and Rider 1972) and *Zonopora* (Nye 1976) spiral branches dichotomize to give daughter branches, one of which spirals in the same direction as the parent branch, and one in the opposite direction.

Further complications in growth pattern occurred when basally extending exozonal growth margins of daughter branches met one another at their confluence with the parent branch. Discrete growth margins belonging to the same *Terebellaria* colony had the ability to coalesce or anastomose on meeting (Pl. 34, fig. 2) and to grow in unison

thereafter. Anastomosis of this type is known to occur in some extant bryozoans and other colonial organisms, and has been termed autosyndrome (Knight-Jones and Moyses 1961; Stebbing 1973; Ryland 1976, pp. 401–409). In *T. ramosissima* the effects of growth margin convergence and anastomosis are difficult to illustrate, as their comprehension ideally requires the use of three dimensions. Diagrammatic external aspects showing three growth stages of three dichotomies are given to illustrate the convergence of two helico-spiral growth margins (text-fig. 13A), a helico-spiral and an annular growth margin (text-fig. 13B), and two annular growth margins (text-fig. 13C).

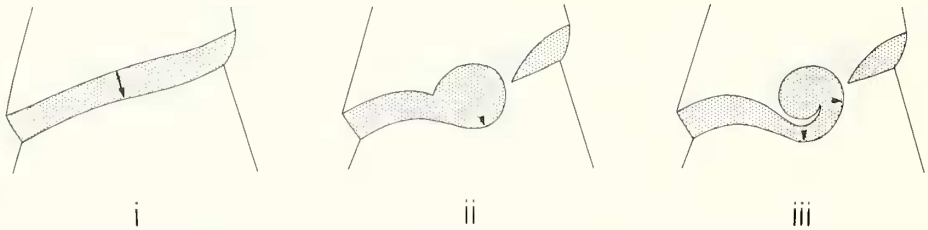


TEXT-FIG. 13. The effect of convergence between basally extending exozonal growth margins of daughter branches at their junction with the parent branch. Diagrammatic external aspects looking down on the distal growth tips. For simplicity and clarity, the effects of angular divergence of daughter branches, and of overlap of more proximal parts of growth margin by autozoocelial ledges (as in text-fig. 1B) have been ignored. Three growth stages ('i'–'iii') are illustrated for each of three examples (A–C). Growth margins and growth tips, stippled; lines of anastomosis, dashed. Circular axial parts of the growth tips are endozones.

A, convergence of helico-spiral exozonal growth margins. At growth stage 'i', the helico-spiral margin of the right-hand daughter branch is continuous with that of the parent branch, but that of the left-hand daughter branch terminates at its confluence with an autozoocelial ledge on the right-hand daughter branch. Further growth ('ii') results in the meeting (m) of helico-spiral growth margins belonging to each daughter branch. Anastomosis between them occurs and causes the development of a discontinuity in the left-hand helico-spiral growth margin. The helico-spiral growth margin of the parent branch now ('iii') appears to be continuous with that of the left-hand daughter branch, whilst that of the right-hand daughter branch abuts against a ledge of autozoecia on the left-hand branch. B, convergence of a helico-spiral growth margin with an annular growth margin. Anastomosis of growth margins occurs when they meet at (ii) (cf. Taylor 1976, text-fig. 5A). Successive annular growth margins are incorporated into the helico-spiral growth margin extending down the parent branch. C, convergence of annular growth margins from daughter branches. Their inclined nature causes anastomosis to be eccentric.

The colonies are viewed from above the growth tips but angular divergence of daughter branches is ignored for it would obscure parts of the parent branch. Anastomosis between growth margins from two spiral daughter branches apparently caused each to be alternately continuous with the spiral growth margin on the parent branch (text-fig. 13A). Successive annular growth margins were absorbed into the spiral growth margin extending down the other daughter branch and the parent branch (text-fig. 13B), whilst pairs of annular growth margins coalesced at their junction with the parent branch (text-fig. 13C) to form a basally extending annulus on the parent branch.

*Secondary or adventitious branching.* Secondary branches usually occur near to the zoarial base and consist of a single small branch arising from a larger parent branch at an angle of about  $90^\circ$  (Pl. 34, fig. 6). Both helico-spiral and annular growth margins have been observed on secondary branches. The former are continuous with growth margin on the parent branch, the latter may subsequently anastomose with growth margin on the parent branch. Zoarial sections reveal that secondary branches are not a product of endozonal dichotomy at the growth tip, but are produced at exozonal



TEXT-FIG. 14. Inferred formation of an adventitious or secondary branch on the exterior of a *Terebellaria* branch in three growth stages ('i'-'iii'). Full explanation in text. Coarse stipple, non-occluded exozonal growth margin; fine stipple, occluded exozonal growth margin; arrows, inferred growth direction.

growth margins by the formation of a secondary endozone approximately perpendicular to and not continuous with the endozone of the parent branch. The inferred sequence of events during formation of a secondary branch are illustrated in text-fig. 14. Firstly, a short length of growth margin became occluded, causing initiation of pivot point-like structures (Taylor 1976) at each end of the occlusion. The growth margin around one of the pivot points broadened (growth stage 'ii') and zooecia began to be formed at divisions of interzooecial walls independent of the budding lamina (i.e. endozonal budding) thus establishing a new endozone. A new series of omega endozonal zooecia formed on the rudimentary secondary branch and extended the budding lamina away from the parent branch with further growth. Frontal walls began to develop (growth stage 'iii') on zooecia of the adventitious branch and eventually exozonal overgrowth commenced.

The occurrence of secondary branches is usually associated with regions of occluded growth margin near zoarial bases. In some cases large zoaria bear two or more secondary branches diverging in different directions from the parent branch. They appear to owe their origin to localized rejuvenation of growth. In other instances



relatively small zoaria, often lacking primary dichotomies, may bear a single secondary branch. These colonies perhaps became detached from their substrate and lay flat on the sea-bed, whereon the adventitious branch formed on the upward-facing side of the colony to renew growth away from the substrate.

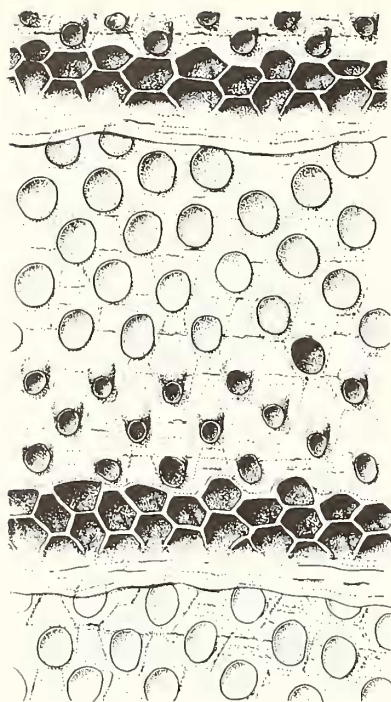
In their relationship with the parent branch, secondary branches are broadly comparable with the 'subsequent-type' branches described from the Palaeozoic cryptostome *Rhabdomeson* (Blake 1976). Subsequent-type branches are thought to have functioned in asexual colony propagation by becoming detached from the parent branch to establish a new 'colony' elsewhere (Blake 1976). Propagation by fragmentation is also known from the cheilostomatous bryozoan *Discoporella umbellata* (Marcus and Marcus 1962) and many colonial anthozoans (e.g. Gilmore and Hall 1976) where it may be of considerable importance during recruitment into new regions. A similar process may have occurred occasionally in *Terebellaria*.

#### EARLY ASTOGENY

The early parts of colony growth in *T. ramosissima* are poorly known. The smallest zoarium examined (BMNH D52636) has an overgrown ancestrula and some trace of initial frontal wall formation. Zoarial sections prepared from the basal parts of *T. ramosissima* zoaria show that the adnate base rapidly gave rise to an erect stem. Initially the endozone was relatively narrow and the helical trace of exozonal origin was tight. Broadening of the endozone was accomplished by increasing the number of endozonal zooecia budded. Development of young colonies compared with secondary branch formation for these also arose from an adnate lamellar base and subsequently developed endozonal budding independent of the budding lamina.

#### ZOOIDAL ONTOGENY

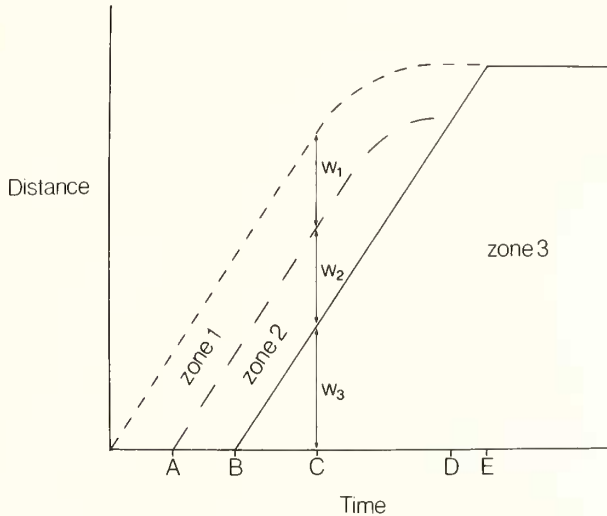
Because older zooids are more distant from the budding region than are younger zooids, bryozoan colonies have an ontogenetic gradient which is directed proximally away from the budding region (Boardman, Cheetham, and Cook 1970). The zooidal ontogeny of *T. ramosissima* is closely comparable to that described for living Diastoporidae (Silén and Harmelin 1974) in which three zones of zooids define distinct stages in an otherwise continuous ontogenetic gradient. Zone 1 is the zooidal budding region or growth margin in which incomplete zooids are enclosed beneath a hypostegal coelom. Zone 2 is composed of zooids which are actively feeding and possess peristomes. Zone 3 comprises zooids which have lost their peristomes and cannot feed because they are sealed by calcareous terminal diaphragms. Skeletal evidence shows that analogous zones existed in *T. ramosissima* colonies during life (Pl. 34, fig. 2; text-fig. 15). Zone 1 is represented by the growth margin and growth tip where zooidal budding occurred and which, by inference, was enclosed within hypostegal coelom. Zooecia having frontal walls, open apertures and peristomes comprise zone 2. As with living Diastoporidae the peristomes of zooecia in *T. ramosissima* colonies increase in height proximally along the ontogenetic gradient. The zooids of zone 2 would have possessed a lophophore and a gut (i.e. a polypide) enabling them to perform a feeding function.



TEXT-FIG. 15. Camera lucida drawing of exozonal zooecia displaying ontogenetic zonation. Zone 1 (the growth margin) is the region of partly formed zooecia. Zone 2 contains zooecia with open apertures and peristomes. In zone 3 zooecia are occluded by terminal diaphragms. The distal fringe of the budding lamina belonging to the growth margin next nearest the branch apex overgrows zone 3; BMNH 11510d, 'Great Oolite, ?locality'.  $\times 28$ .

An abrupt loss of peristomes and occlusion of zooecial apertures occurs between zones 2 and 3 in *T. ramosissima*. These changes are analogous to those accompanying polypide degeneration in extant Diastoporidae. Gregory (1896*a, b*) termed the occluded zooecia of zone 3 in *T. ramosissima* dactylethra, but did not fully understand their ontogenetic significance, interpreting them instead as heterozooecia. The calcareous diaphragms which cover apertures of zone 3 zooecia possess pseudopores, indicating that they are part of a calcified exterior body wall and are equivalent to the terminal diaphragms defined by Nye (1968). Although known from other bryozoan taxa (see Ryland 1970, pp. 59-60), polypide regeneration apparently did not occur in *T. ramosissima*, there being no evidence indicating the necessary resorption of terminal diaphragms proximal to zone 3. Localized absence of zone 2, leaving zone 3 in juxtaposition with the growth margin, is not uncommon in *T. ramosissima*. Occlusion of the growth margin (Pl. 34, fig. 3) by typical calcified exterior body wall (with pseudopores) which completely covers the ends of partly formed zooecia occasionally accompanies absence of zone 2. Loss of the hypostegal coelom and calcification of the terminal membrane (Boardman and McKinney 1976) was probably necessary to occlude the growth margin. If renewed zooidal budding were to occur, the calcified portion of the exterior body wall would first have to be resorbed. Progressive occlusion of growth margin distant from the growth tip occurred in most zoaria examined. Extensive lengths of occluded growth margin may be completely overgrown near the colony base by active growth margin derived from the growth tip at an astogenetically later stage.

Absence of the zone of open zooecia and occlusion of the growth margin can be explained by variations in the relationship between zooidal budding rate (equivalent to the astogenetic or colony growth rate) and the time required for a zooid to reach skeletal maturity (ontogenetic rate). It is thought that variations in the former were probably more pronounced than variations in the latter, and for simplicity the ontogenetic rate has been made constant in text-fig. 16 which explains the relationship between ontogeny and astogeny in *Terebellaria* (and other tubuloporinid cyclostomes).



TEXT-FIG. 16. Time-distance plot explaining the possible relationship between astogeny and ontogeny. The ontogenetic rate (rate at which zooidal structural maturity is reached) is held constant but astogenetic rate (colony growth rate) is allowed to vary. Short dashes, distal edge of the growth margin; long dashes, distal edge of zooecial frontal walls; solid line, line of occlusion. Zone 2 first appears at time A with the formation of the first zooecial frontal walls. Zone 3 appears at time B when zooecial occlusion commences. At time C the width of zone 1 is  $W_1$ , zone 2 is  $W_2$ , and zone 3 is  $W_3$ . The astogenetic rate is made to gradually decrease after time C. As a result zone 2 becomes progressively narrower before disappearing at time D. Zone 1 subsequently becomes occluded and is completely occluded at time E.

Text-fig. 16 is a time-distance graph on which is plotted the position of the most distal part of the growth margin (dependent on astogenetic rate), the position of the most distal frontal wall (marking the zone 1-2 boundary), and the position of the most distal occluded zooecium (related to ontogenetic rate). The origin of the graph represents the first formed part of the colony, the protoecium. From the protoecium the colony expands distally by extension at the growth margin (zone 1) and zone 2 comes into existence at time A when the first frontal wall is formed. Occlusion of zooecia first occurs at time B initiating zone 3. During normal growth, zones 1 and 2 maintain a constant width but zone 3 widens as the colony expands distally. In text-fig. 16 the rate of zooidal

budding or astogenetic rate is shown to decrease after time C. Observations show that the growth margin does not narrow significantly suggesting that decrease in astogenetic rate is accompanied by decrease in the rate of advance of the most distal frontal wall. However, the ontogenetic rate, as portrayed by distal expansion of zone 3, is not affected by reduction in astogenetic rate. Consequently, zone 2 narrows until it eventually disappears altogether at time D. Zone 1 subsequently decreases in width as the growth margin becomes occluded until it is fully occluded by time E. In reality, a considerably more complex relationship between astogeny and ontogeny probably existed. Indeed, it is often difficult to make a distinction between morphological variations between zooids due to different ontogenetic states and those due to astogeny (Cook in press).

Cessation of zooidal budding near the colony base may have been determined by environmental factors, for example, shortage of food or the presence of muddy sediment at low levels around the colony. Alternatively, it may have related to a decrease in growth vigour dependent on distance from the growth tip and perhaps indicative of hormonal control of growth from growth centres at the branch apices comparable with postulated hormonal control of growth in Palaeozoic trepostomes (Anstey, Pachut, and Prezbindowski 1976).

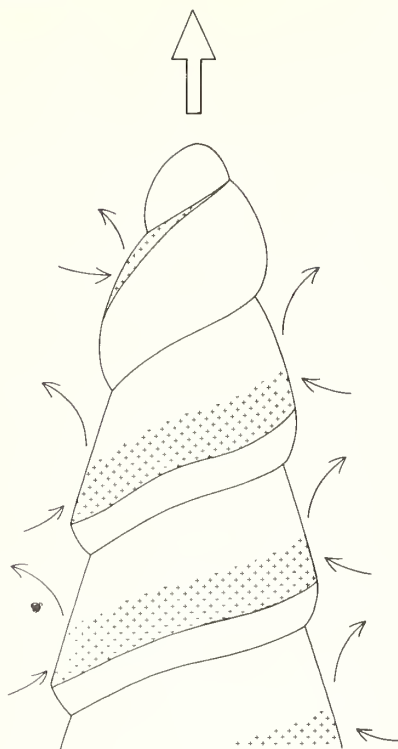
#### COLONIAL WATER CURRENTS

The ability of living bryozoan colonies to produce colonial water current systems has recently been recognized (Banta, McKinney, and Zimmer 1974; Cook 1977). Physical co-operation between zooids enables a colonial water current system to be created, probably for a variety of purposes, including enhancement of over-all colony feeding ability, spermatozoan and larval dispersion, and for cleaning the colony surface of sediment. A functional morphological approach (Rudwick 1964) can be applied to fossil zoaria in an attempt to reconstruct colonial water current systems which may have been operative during the life of the bryozoan (e.g. Cowen and Rider 1972). The key premise is that individual zooids in colonies of extinct bryozoans created the same type of feeding currents as those which have been observed from zooids in living bryozoan colonies. In living bryozoans cilia on zooidal tentacles beat to create a current which draws water in at the top of the tentacle crown (Borg 1926, figs. 10-12; Ryland 1970, fig. 6) and passes exhalant water out laterally between the tentacles. Zooids may combine their individual feeding activity to produce currents operating at subcolonial or colonial level. For example, a net exhalant flow has been observed to occur in *Membranipora* sp. over areas of the colony from which zooidal tentacle crowns lean outwards (Banta *et al.* 1974).

It has been inferred that in *T. ramosissima* feeding zooids occupied a band (zone 2) about 1 mm wide immediately proximal to the growth margin. Within this band, peristomes lean towards the growth margin and increase in height away from the growth margin. The inclination of the peristome determines the attitude of the tentacle crown for the tentacle crown itself is too short to lean significantly in cyclostomes (Banta *et al.* 1974). Hence, zooidal lophophores in *T. ramosissima* colonies probably leaned towards the growth margin and were raised gradually higher above the colony surface with increasing distance from the growth margin as peristome height increased



TEXT-FIG. 17. Colonial water current system inferred to have developed along *Terebellaria* branches during life. Small arrows indicate the over-all direction of water flow created by the co-operative action of feeding zooids within zone 2 (indicated by crosses). A distal flow of water exchanged between consecutive bands of feeding zooids may have resulted in a net exhalant flow above the branch apex (large arrow).



towards zone 3. An orientation and distribution of tentacle crowns of this nature would have resulted in a net inhalant flow approaching zone 2 obliquely from the direction of the growth margin (text-fig. 17). The predominant exhalant discharge of water would have been directed towards zone 3 as it rose away from the surface of the colony. The current system would have been repeated several times along each branch, with repetition of the zone of feeding zooids corresponding to each helico-spiral whorl or each annulus. Some exchange of water between zooids in successive bands may have resulted in a general flow of water from the base towards the apex of each branch. Spermatozoan and/or larval dispersion in particular would benefit from expulsion of water over branch tips. The fairly uniform distance maintained between successive whorls or annulae of inferred feeding zooids supports the postulated existence of a colonial water current system during life. The mean distance between whorls or annulae of 2.23 mm (standard deviation = 0.543 mm) determined from 197 measurements made on thirty-five zoaria is similar to known intermonticular distances and distances between exhalant chimneys in *Membranipora* sp. (Banta *et al.* 1974; Taylor 1975).

#### PALAEOECOLOGY

Despite the abundant preservation of zoarial bases, only rarely are they found adhering to a substratum. Bases of attachment tend to be fairly flat over-all but finely crinkled, with the outermost zoecial layers often inturned at the periphery of the base.

This evidence suggests that most colonies were attached to a perishable (presumably organic) substrate and that inturning of outer zooecial layers may have occurred as a response to decomposition of the substrate.

Colonies from the Bradford Clay of Bradford-on-Avon in Wiltshire are thought to have been a constituent of the fauna associated with the upper surface of a hardground which underlies the clay (Palmer and Fürsich 1974). In Normandy, *Terebellaria* occurs in both cross-bedded oobiosparites and calcareous clays. Colonies probably required environments of stabilized sediment but where current action was sufficient to ensure good water circulation. Their occurrence in clay-rich lithologies may be explained by the often pelleted nature of the clay increasing its coherence and lessening turbidity (Palmer 1974), or by the argillaceous sediment being a later sudden influx. Post mortem breakage and abrasion of zoaria is common, particularly in the Bradford Clay specimens. Zooecial chambers exposed at breakages are sediment-filled rather than calcite-filled, and frontal walls may be worn away. Fractured and worn surfaces may be encrusted by epifauna. Fracturing of colonies often occurred at places where they had been bored into by small lithophagid bivalves. *Terebellaria* zoaria also frequently bear slit-shaped borings, probably made by acrothoracic cirrepeds (Cook 1968, p. 146) and an adnate epifauna dominated by serpulids and bereniciform bryozoans. It seems that most of the attached fauna developed after death of the *Terebellaria* colony, for only rarely is an epifauna immured between exozonal layers. During life, constant overgrowth of the colony surface by successive exozonal layers would have allowed little opportunity for the establishment of an exogenous epifauna. However, regular exozonal layering is occasionally disturbed, possibly by the action of external agencies, and the damage may be covered by subsequent exozonal overgrowth.

In over-all size and proportions, *Terebellaria* zoaria are strikingly similar to the thick branched dendroid cerioporinid cyclostomes abundant in the Bathonian of Normandy. They probably fulfilled a similar ecological role to one another and competed for similar resources. Their similar zoarial forms were, however, produced in distinctly different ways. Cerioporinids retained a hypostegal coelom over their colony surface throughout astogeny and could increase branch diameter by extending existing interzooidal walls. *Terebellaria* achieved the same result of increasing branch diameter by forming a succession of basally directed overgrowths.

#### SYSTEMATIC DESCRIPTION

- Phylum BRYOZOA Ehrenberg, 1831
- Class STENOLAEMATA Borg, 1926
- Order CYCLOSTOMATA Busk, 1852
- Suborder TUBULOPORINA Milne-Edwards, 1838
- Family ?DIASTOPORIDAE Busk, 1859
- Genus TEREPELLARIA Lamouroux, 1821

*Type species. Terebellaria ramosissima* Lamouroux, 1821, by monotypy.

*Terebellaria ramosissima* Lamouroux, 1821

Plates 34, 35; text-figs. 6, 9, 15

- 1821 *Terebellaria ramosissima* Lamouroux, p. 84, pl. 82, fig. 1.  
 1821 *Terebellaria antilope* Lamouroux, p. 84, pl. 82, figs. 2-3.  
 1825 *Terebellaria antilope* Lamouroux; Bronn, p. 20, pl. 6, fig. 13A-B.  
 1828 *Terebellaria antilope* Lamouroux; DeFrance, p. 112, pl. 45, fig. 6.  
 1830 *Terebellaria ramosissima* Lamouroux; de Blainville, p. 374, pl. 45, fig. 5, 5a.  
 1834 *Terebellaria ramosissima* Lamouroux; de Blainville, p. 409, pl. 67, fig. 5, 5a.  
 1834 *Terebellaria antilope* Lamouroux; de Blainville, p. 409, pl. 67, fig. 6.  
 1837 *Terebellaria antilope* Lamouroux; Bronn, p. 246, pl. 16, fig. 12A-B.  
 1845 *Terebellaria ramosissima* Lamouroux; Michelin, p. 231, pl. 55, fig. 10.  
 1845 *Terebellaria antilope* Lamouroux; Michelin, p. 232, pl. 55, fig. 11.  
 1850 *Terebellaria tenuis* d'Orbigny, p. 318.  
 1851 *Terebellaria antilope* Lamouroux; Bronn and Roemer, p. 93, pl. 16, fig. 12.  
 1853 *Terebellaria antilopa* Lamouroux; d'Orbigny, p. 885, pl. 763, figs. 14-18.  
 1854 *Terebellaria ramosissima* Lamouroux; Haime, pp. 173-175, pl. 6, fig. 12C-I only.  
 1857 *Terebellaria ramosissima* Lamouroux; Pictet, p. 141, pl. 91, fig. 17.  
 1881 *Terebellaria ramosissima* Lamouroux; Quenstedt, p. 227, pl. 151, fig. 69.  
 1896a *Terebellaria ramosissima* Lamouroux; Gregory, p. 292.  
 1896b *Terebellaria ramosissima* Lamouroux; Gregory, pp. 188-191, text-figs. 16-17, pl. 10, fig. 5.  
 1922 *Terebellaria ramosissima* Lamouroux; Canu and Bassler, p. 34, pl. 10, figs. 7-8, 10-19 only.  
 1952 *Terebellaria ramosissima* Lamouroux; Buge, p. 699, figs. 45-46.  
 1953 *Terebellaria ramosissima* Lamouroux; Bassler, p. G54, fig. 22, 1A-C.  
 1967 *Terebellaria ramosissima* Lamouroux; Walter, p. 40, pl. 9, fig. 3.  
 1968 *Terebellaria tenuis* d'Orbigny; Walter, p. 7, pl. A, fig. 9.  
 1969 *Terebellaria ramosissima* Lamouroux; Walter, pp. 130-132, pl. 8, figs. 6-10; pl. 9, fig. 1.  
 1972 *Terebellaria ramosissima* Lamaroux; Tavener-Smith and Williams, pp. 132-135, figs. 125-127, 131.

*Material.* Numerous zoaria from the localities mentioned below, many of which will be deposited in the collections of the BMNH. The following specimens, including all figured material, are from the BMNH collections (supposed localities and horizons are given in Gregory 1896b, p. 191; numbers in brackets indicate the number of zoaria per catalogue number):

11510(8), 23857, 24768(2), 24958, 60214, 60215, 60215a-g, 60361, 60382, B163, B2281(5), B4645(3), B4646(5), B4647(3), B4648, B4649, D25(3), D1762, D1812(17), D1823(2), D2110(3), D2111, D2112, D2160, D2165, D2169, D2214, D2240, and 60360(3), B4577(3) 'Bathonian, Ranville'; D1982 'Bradford Clay, ?locality'; D47408 'Jurassic, ?locality'; D52636 Upper Bathonian, Amfreville; D52637 Upper Bathonian, St. Aubin-sur-mer.

*Type.* According to Walter (1969), Lamouroux's type specimen was destroyed during the destruction of Caen University in 1944. A neotype from the Upper Bathonian of St. Aubin-sur-mer, Normandy was designated by Walter (1969) and is number 28638 in the collections of the Département des Sciences de la Terre, Lyon.

*Revised diagnosis.* Tubuloporina with an endozone of erect zooecia which at the branch apices gives rise to a multilamellar exozonal overgrowth of zooecia directed proximally towards the colony base.

*Description.* Zoaria erect and dichotomously branched. Smaller branches may develop proximal to the zoarial apex, diverging at about 90° from the parent branch. A multilamellar exozone arises from apical growth tips to form a basally directed overgrowth around a cylindrical endozone. The exozonal budding lamina originates where axial interzoecial walls of a particular row of endozonal zooecia (the omega zooecia) divide at the circumference of the endozone. The overgrowth may occur from a helico-spiral growth margin or, less commonly, from a succession of annular growth margins. Endozonal autozooecia are budded interzoecially at triple junctions between previously existing interzoecial walls. The locus of

endozonal autozoecial budding occurs above the axial walls of omega zooecia and rotates with zoarial extension. Exozonal autozoecia form at divisions of existing interzoecial walls on a basal budding lamina of exterior body wall. Exozonal autozoecia are rather thinner-walled, more angular in cross-section and have shorter frontal walls than endozonal autozoecia. Autozoecia have short frontal walls, commonly six-sided, with a large, slightly longitudinally elongate aperture situated distally. Long, distally tapering peristomes are lost in later ontogeny and the aperture becomes occluded by a terminal diaphragm bordered by a slightly raised rim. Intrazoecial structures include occasional thin-walled, non-terminal diaphragms and some cystiphragm-like structures. Kenozoecia are infrequent, although some apparent kenozoecia which lack any trace of an aperture occur particularly near the zoarial base. Only a small proportion of zoaria bear ovicells. The ovicell is an inflated gonozoecium which is transversely elongate and has a small, terminal, transversely elongate ooeciopore (Pl. 34, fig. 8).

TABLE 1. Dimensions of exozonal autozoecial characters. Nc, number of colonies considered; Nz, total number of zooecia measured (at least fifteen per colony);  $\bar{x}$ , mean value in mm calculated by averaging within colony means; SD, standard deviation in mm; CV, coefficient of variation ( $100 \times SD \div \bar{x}$ ); rc, range of colony means in mm; rz, range of zooecial values in mm. Abbreviations for characters given in text-fig. 18.

Character	Nc	Nz	$\bar{x}$	SD	CV	rc	rz
ldw	30	738	0.20	0.018	8.8	0.16-0.23	0.11-0.31
tdw	30	738	0.17	0.012	7.3	0.14-0.18	0.10-0.22
fwl	11	269	0.38	0.096	25.3	0.29-0.55	0.19-0.94
fww	11	269	0.25	0.017	6.8	0.22-0.27	0.18-0.33
law	—	—	c. 0.14	—	—	—	—
taw	—	—	c. 0.11	—	—	—	—

TABLE 2. Dimensions of ovicellular characters. Nc, number of colonies considered; No, number of ovicells measured;  $\bar{x}$ , mean value in mm calculated by averaging the summed data from all ovicells; SD, standard deviation in mm; CV, coefficient of variation; r, range of values in mm. Character abbreviations; lo, length of ovicell frontal wall; wo, width of ovicell frontal wall; low, longitudinal ooeciopore width; tow, transverse ooeciopore width.

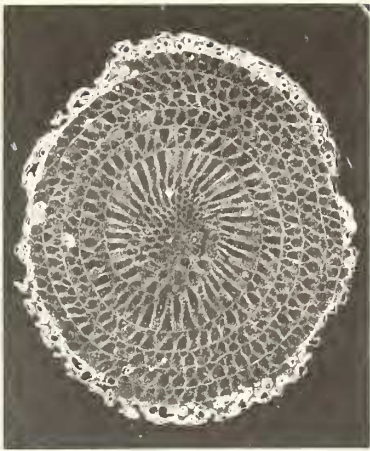
Character	Nc	No	$\bar{x}$	SD	CV	r
lo	11	30	0.88	0.210	24.0	0.48-1.22
wo	11	37	2.01	0.482	24.0	0.99-2.92
low	7	10	0.09	0.024	27.3	0.06-0.13
tow	7	10	0.14	0.035	25.5	0.10-0.20

#### EXPLANATION OF PLATE 35

Figs. 1-7. *Terebellaria ramosissima* Lamouroux. Bathonian, Ranville. 1, BMNH 60215c, transverse section of branch with sinistral helico-spiral growth margin,  $\times 6.4$ . 2, BMNH D2111f, longitudinal zoarial section; compare with text-figs. 2A and 7,  $\times 9.5$ . 3, BMNH D2111d, transverse zoarial section in the vicinity of a branch dichotomy. The uppermost daughter branch displays annular exozonal growth, the lowermost displays spiral exozonal growth,  $\times 6.3$ . 4, BMNH 60215c(8), endozonal budding on the axial wall of an omega zooecium (arrowed), and the transition between endozone and exozone; compare with text-fig. 6B,  $\times 41$ . 5, BMNH D2111k, exozonal layers with zooecia cut transversely,  $\times 36$ . 6, BMNH D2111d, an interzoecial wall with a pore (arrowed) dividing into two zooecial frontal walls overgrown by the basal lamina of a succeeding exozonal layer,  $\times 244$ . 7, BMNH D2111d, zooecial frontal wall with two pseudopores (lower centre) covered by the basal lamina (arrowed) of a succeeding exozonal layer,  $\times 646$ .

Figs. 1-3 are negative photographs prepared from acetate peels. Figs. 4, 5 are light photomicrographs of acetate peels. Figs. 6, 7 are scanning electron photomicrographs of an etched specimen.





1



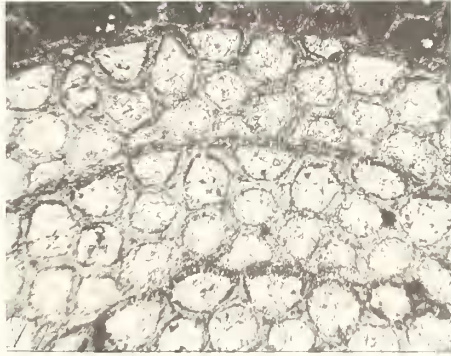
2



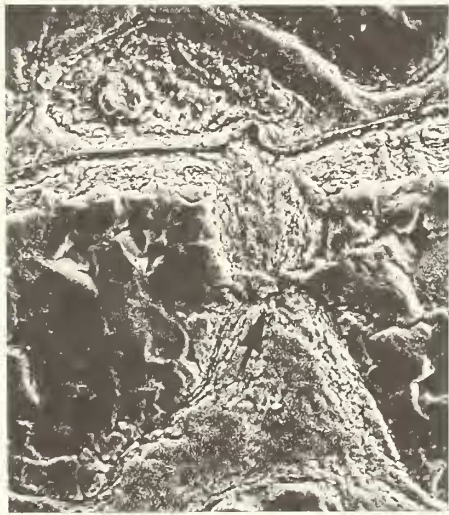
3



4



5



6



7

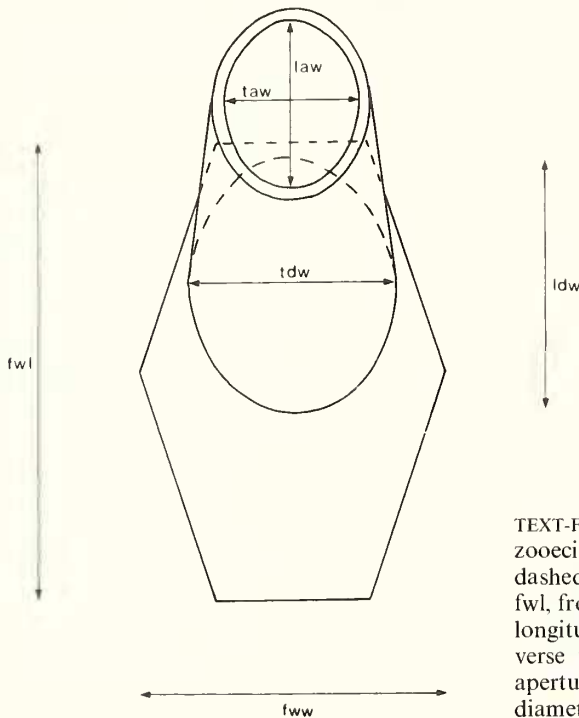
TAYLOR, *Terebellaria ramosissima*

*Remarks.* As Walter (1969) pointed out, Lamouroux's (1821) two species of *Terebellaria*, *T. ramosissima* and *T. antilope*, are synonymous. *T. antilope*, the junior synonym, was used for slender zoaria, and *T. ramosissima* for zoaria with broad branches. Differences of this nature may be astogenetic (related to colony age) or ecophenotypic, and can be explained by the growth model here proposed.

*T. ?increscens* Vine, 1884 is probably a form of *Reptomultisparsa microstoma* (Michelin, 1845) (see Walter 1969, pp. 80-81) possessing erect *Pustulopora*-like branches which were subsequently covered by intracolony lamellar overgrowths, giving the appearance of a multilamellar exozone. The overgrowths do not, however, originate at apical growth tips, and the axial erect portion of the zoarium has a symmetrical appearance in zoarial transverse section, contrasting with that of *T. ramosissima*. Zoarial longitudinal sections reveal, in contrast to *T. ramosissima*, the erect axis of the zoarium and the multilamellar peripheral overgrowths separated by exterior body wall. This form of *R. microstoma* is more abundant than *T. ramosissima* in bradfordian facies deposits of England and probably has been frequently misidentified as *T. ramosissima*, judging from museum collections examined.

Although the suborder Tubuloporina (see Brood 1972, p. 174) is not totally satisfactory as presently understood, *Terebellaria* is provisionally classified with that suborder in accordance with Walter (1969) for the following reasons:

1. A conventional 'single-walled' (Borg 1926) mode of growth (equivalent to stictocystic growth of Ryland 1970, and fused-wall growth of Boardman 1976) is inferred from the presence of typical zooecial frontal walls (Pl. 35, fig. 7) composed of exterior body wall. *Terebellaria* cannot be classified with the two



TEXT-FIG. 18. Diagram of a *Terebellaria ramosissima* zoecium to show the characters measured. Detail is dashed where obscured when a peristome is present. fwl, frontal wall length; fww, frontal wall width; ldw, longitudinal terminal diaphragm width; tdw, transverse terminal diaphragm width; law, longitudinal apertural diameter; taw, transverse apertural diameter.

other single-walled cyclostome suborders Articulata and Salpingina respectively, for it lacks articulating nodes between internodes of zoecia, and does not possess avicularia-like polymorphs or operculate autozoecia.

2. The ultrastructure of the interzoecial walls consisting of a granular layer flanked by laminar layers is of Brood's (1972, p. 33) tubuloporinid type.

3. The ovicell is an inflated gonozoecium typical of tubuloporinidean ovicells.

4. The sequence of ontogenetic changes, apparent from autozoecial characteristics, compares closely with those described from an extant family of tubuloporinideans by Silén and Harmelin (1974).

The suggestion that *T. ramosissima* is a rectanguloid has been made by Tavener-Smith and Williams (1972, p. 135). Their interpretation, however, appears to be founded on an erroneous comprehension of its three-dimensional zoarial form (cf. fig. 131 of Tavener-Smith and Williams with text-fig. 7 here).

*Stratigraphical range* (according to Walter 1969). Upper Aalenian (*concauum* Zone) to Lower Callovian (*macrocephalus* Zone).

*Confirmed occurrence*. Southern England. Bathonian: Upper Rags, Great Oolite (*aspidoides* Zone), Bathampton Down, Somerset (ST776653); Forest Marble (*aspidoides* Zone), Fault Corner, Bridport, Dorset (SY453908); Bradford Clay (*discus* Zone), Canal Quarry, Bradford-on-Avon, Wiltshire (ST826600).

Normandy, France. Bathonian (lithostratigraphical divisions and ammonite zones after Palmer 1974): Fontaine-Henry Member (*morrissi* and *subcontractus* zones), Fontaine-Henry (T979786); Blainville Member (*morrissi* to *aspidoides* zones), Blainville (U080731); Campagnettes Member (*aspidoides* Zone), Carriere des Campagnettes Ranville (U114748); St. Aubin Member (*aspidoides* Zone), Amfreville (U121760), Carriere des Campagnettes Ranville (U114748), Reviens (T957818) (considered to be St. Aubin Member rather than Fontaine-Henry Member, Palmer pers. comm. 1976), St. Aubin-sur-mer (T851015); Langrune Member (*discus* Zone, *hollandi* Subzone), Douvres la Deliverande (U032815), Luc-sur-mer (U054850), Commeaux (U228233), Occagnes (U232238).

## DISCUSSION

*Terebellaria* displays a growth form which would appear to be unique amongst bryozoans. No other taxa are known to combine an essentially erect framework with an apically diverging, characteristically spiral, overgrowth. Spiral, or more correctly, helical budding sequences do, however, occur in numerous other erect cyclostomes, e.g. *Spirentalophora* (McKinney 1975), *Spiropora* (Voigt and Flor 1970), and *Zonopora* (Nye 1976). In *Spiropora* some branches have a helical zoecial budding sequence reflected by helical arrangement of apertures on the colony surface, but other branches have a periodic sequence of zoecial budding giving rise to an annular arrangement of apertures on the colony surface. A similar flexibility of growth is displayed by *Terebellaria* in which continuous helical endozonal budding and periodic annular endozonal budding produce branches which have a spiral overgrowth and annular overgrowths respectively in the same colony. This type of intracolony growth variation seems anomalous because other morphological features imply a precise pattern of growth involving considerable colonial co-ordination. The presence of a hypostegal coelom is usually taken to indicate a high degree of colony dominance over individual autonomy (Boardman and Cheetham 1973). Thus a higher degree of colony dominance may be expected within the common bud than in areas away from the common bud. It follows that colonial co-ordination of growth within one particular area of common bud should be greater than colonial control of growth between discrete areas of



common bud separated by areas of the colony lacking hypostegal coelom. Hence, discrete common buds may be expected to function semi-autonomously. Therefore, in *Terebellaria*, over-all organization of growth in colonies with a solitary helico-spiral growth margin should have been considerably greater than in colonies with annular growth margins each functioning semi-autonomously.

As in many other animals which secrete an accretionary skeleton (see Gould 1970), the relatively intricate three-dimensional morphology of *Terebellaria* is the product of a few comparatively simple 'rules' of growth. The involved form of *Terebellaria* may be synthesized given that:

1. Axial walls of a row/rows of endozonal zooecia (omega zooecia) which arose nearest to the centre of the endozone functioned as the locus of endozonal budding.
2. The locus of endozonal budding rotated during growth.
3. Axial walls belonging to the row/rows of endozonal zooecia (omega zooecia) which arose nearest to the endozone centre dichotomized into a frontal wall and a budding lamina on meeting the surface of the cylindrical endozone.
4. Previously formed zooecia were overgrown by exozonal zooecia arising on the basally extending budding lamina.

Many unusual morphological features of the zoarium are a necessary consequence of the aberrant growth mode. For example, endozonal zooecia must fill the spaces between successive whorls described by the helical row of omega zooecia, or successive annulae described by consecutive rows of omega zooecia. In order to do so, endozonal zooecia budded further distally within each whorl or annulus make successively greater angles with the zoarial axis (text-fig. 7). The result is that the total length of endozonal zooecia decreases but their frontal wall length increases away from the endozonal axis towards the contiguous exozone. The use of morphological features of this type as independent characters in taxonomic descriptions may therefore be questioned. By applying a more dynamic description of morphology such superfluous characters can be eliminated.

*Terebellaria* probably possessed a number of functional attributes which would have conferred selective advantage under certain environmental conditions. Multi-lamellar exozonal growth allowed older portions of the colony lacking feeding zooids to be overgrown by younger portions of the colony with feeding zooids. Moreover, the erect endozonal framework, probably produced at a relatively high cost in terms of energy expenditure, functioned secondarily as a support for subsequent exozonal growth. Thus, a large part of the colony, the exozone, enjoyed the low energy expenditure of adnate growth but gained many of the advantages of erect growth, in particular, freedom from the spatial competitive restrictions of an external substratum. Basally extending exozonal overgrowths strengthened the colony near to the zoarial base where most required, whilst also restricting colonization of the bryozoan by epifauna and boring organisms. A further selective advantage was probably bestowed by the colonial water-current system, which would have enhanced colony feeding efficiency and aided spermatozoan and larval dispersal.

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